SELENOMONAS BOSKAMP, 1922—A GENUS THAT INCLUDES SPECIES SHOWING AN UNUSUAL TYPE OF FLAGELLATION

ERWIN F. LESSEL, JR. AND ROBERT S. BREED

Cornell University, Geneva, New York

In revising the 6th edition of Bergey's Manual (1), a study has been made of the validity of the genus *Selenomonas* Boskamp (2). This generic name was introduced into the literature by von Prowazek (3) in 1913. However, he did not name any species as belonging in the genus, and the name did not have a valid status until Boskamp (2) described the species *Selenomonas palpitans* from the caecum of a guinea pig. This species had been named earlier (1921) by Simons (4), but he failed to give a description so that the organism did not receive a valid name until Boskamp (2) published a description of it, ascribing the description to Simons.

The species mentioned above includes organisms that are unique in their type of flagellation. These organisms have been generally overlooked as they are strictly anaerobic and do not grow readily on the media that were used by early investigators. It is little wonder that a poorly described genus and a species introduced into the literature with so little regard for the conventions established by codes of nomenclature have been so generally ignored.

Selenomonas palpitans is, however, a species in which the organisms are sufficiently characteristic in their appearance and habitat to make even a microscopic description adequate for identification. The cells are of crescent form with blunt ends and are spirally twisted when they remain in chains. Thus they show the normal appearance of organisms belonging to the genus *Spirillum*. However, the cells are motile with a curious tumbling type of motility different from that of the ordinary spirillum. Staining with Giemsa's stain by von Prowazek (3) revealed what appeared to be a single, red-stained, very heavy flagellum attached at the middle of the concave side of the cell. Further studies showed this stout flagellum to be in reality a tuft of perhaps a dozen individual flagella. As shown in a related species from the human mouth in separated form in electron micrographs by Macdonald (5), the flagella may readily be thought of as attached peritrichously, and they have been so reported by a few investigators. When examined by dark field microscopy and as stained by Giemsa's stain, the attachment of the flagella in the center of the concave side becomes clear. A highly refractive body within the cell absorbs nuclear stains and apparently is a nuclear body. The cell structure and unique form of flagellation fully justify the recognition of this species as the type species of a genus distinct from *Spirillum*.

Because of the anaerobic nature of these organisms, investigators have not succeeded in cultivating them very readily, and their physiological characteristics were not well known until Macdonald (5) succeeded in cultivating the mouth organism anaerobically in reduced blood agar and Difco thioglycolate broth.

Selenomonas palpitans apparently occurs not only in the intestinal tract of guinea pigs, but also in the intestine of related rodents and herbivorous mammals. It, or a closely related species, has been found by von Prowazek (3) in examinations of blood contaminated with fecal matter of gazelles, giraffes and antelope shot in Africa (3). It has also been found in Brazil (6) in a rodent related to the guinea pig (*Cavia sperea*) and in a deer (*Caryacus* sp.).

The recognition of the genus *Selenomonas* is also indicated by the history of another species of bacteria that has been known for an even longer time than *Selenomonas palpitans*. In fact, Dobell (7), in his book describing the work of van Leeuwenhoek, feels confident that this organism was one of those found in the human mouth by this investigator in his original description of bacteria from the mouth. This species from the human mouth, which has been named *Spirillum sputigenum* since 1886 (8), shows a tumbling, rotary motion. Because of this characteristic movement van Leeuwenhoek was led to draw the path of this organism in his original drawing as a curved, dotted line with a loop in it (7).

It has been difficult to determine who first used the binomial *Spirillum sputigenum*. How-

ever, it seems probable that Miller, an American dentist, originated the name during the course of his work that resulted in the publication of his inaugural dissertation from the University of Berlin. Apparently Flügge (8) knew of Miller's work and used the name (without giving its origin) in the second edition of his textbook (1886). This is the first use of the binomial *Spirillum sputigenum* that we have found, and it is accompanied by a description of the species. Miller's dissertation (9) was not published until 1887. No copy of this has been found, but he probably described *Spirillum sputigenum* in it. At least he uses this binomial and describes this species in the various editions of his book on mouth organisms (10) that is based on this thesis. In subsequent literature Miller is usually given as the author of this binomial.

Miller did not succeed in cultivating this species from the human mouth, but he and various other investigators studied it microscopically. It soon was established (11, 12, 13, 14) that this crescent-shaped organism had a tuft of flagella attached laterally. This morphology is exactly similar to that described for *Selenomonas palpitans*, and therefore Dobell (7) placed *Spirillum sputigenum* in the genus *Selenomonas* in 1932. The latter species, however, was not well described until Macdonald (5) published his thesis. Like *Selenomonas palpitans* it is a strict anaerobe.

Protozoologists have reported the presence of still another organism in the rumen juice of herbivorous mammals (cattle, sheep, deer and especially goats) that is similar to *Selenomonas sputigena* and *S. palpitans*. Certes (15) observed these in 1889 and, because of certain resemblances (S-form when in chains) to the protozoan species *Ancyromonas sigmoides* Kent, named these crescent-shaped forms *Ancyromonas ruminantium*.

Kerandel (16) also found this so-called *Ancyromonas* in the blood of an antelope (*Cephalophus* sp.) that was contaminated with stomach contents. The animal was shot in the Congo Region of Africa.

Later Woodcock and Lapage (17) found these organisms in the rumen juice of various domestic animals and placed them in a new genus *Selenomastix* under the name *Selenomastix ruminantium* (Certes) Woodcock and Lepage. The latter authors were confident that the organisms in question were not true protozoa and reported that they were like spirilla in many ways, though they were doubtful whether they should be regarded as bacteria. They concluded that these flagellated crescents were an unusual primitive type and listed them as a sort of "Pro-flagellate".

The crescents from the rumen are described in the foregoing papers as having a morphology like that of the organisms placed in the genus *Selenomonas*. They normally have a stout flagellum attached in the center of the concave side of the crescent, and the organisms divide by transverse fission. When this happens, the flagellum divides lengthwise and for a time the two flagella are attached near the blunt ends of the more or less pear-shaped young cells. The flagella stain red with Giemsa's stain and then show that they are divided into fibrils as if the stout flagellum really represented a tuft of flagella. The cells show several refractive bodies flattened against the cell membrane; these granules stain with chromatin stains and may be nuclear in character. Occasionally the granules lie underneath the point where the flagella are attached as is also stated to be true in *Selenomonas palpitans*.

Because Woodcock and Lapage (17) build up a doubtful life cycle for the rumen organisms and because other characteristics are not exactly like those of *Selenomonas sputigena* or of *Selenomonas palpitans*, the rumen species is accepted for the present as a third species in *Selenomonas*. The movements of the rumen organisms are described in terms similar to those used in describing the movements of the species previously placed in *Selenomonas*, and the body of the organism is reported to have the power of movement independent of any action of the flagella. On this account, the possibility that these organisms may have affinities with the spirochaetes is discussed (see next section).

Textbooks of protozoology by Wenyon (18) and by Neveu-LeMaire (19) describe these unusual crescent-shaped organisms. Wenyon placed them in the genus *Selenomonas* under the name *Selenomonas ruminantium* (Certes) Wenyon, and they are described under this name as recently as 1948 by McGaughey and Sellers (20).

DISCUSSION

From this review it is evident that three quite different groups of workers, (a) students of oral bacteriology, (b) investigators of intestinal

bacteriology, and (c) protozoologists, have all found and named these flagellate organisms. The organism found in the human mouth has been named *Selenomonas sputigena* and has been cultured anaerobically on Difco thioglycolate media by Macdonald (5) in a way that demonstrates that it should be regarded as a bacterium. The organism found in the rumen juice of herbivorous mammals has been named *Selenomonas ruminantium*; it has not been cultured and is not well known even to recent students of rumen bacteriology though it is well known to protozoologists. The organism found first in the caecum contents of guinea pigs (which is named *Selenomonas palpitans*) has later been shown to be common in the intestines of both rodents and herbivorous mammals. As these bacteria swim by means of a tuft of flagella and have also been claimed to have the power to move independently of the flagella (2), they may well represent organisms intermediate between *Spirillum* and *Spirochaeta*, thus indicating a close relationship between the species placed in *Spirillaceae* and those placed in *Spirochaetaceae*.

In view of the similar morphology and the limited cultural studies that have been made on the three species included in this genus, it is, of course, possible that all of these species are identical; but for the present it is believed desirable to regard them as separate species. It may even be possible that further studies may show that additional species should be recognized.

CONCLUSIONS

Selenomonas von Prowazek, 1913, *emend.* Boskamp, 1922, is a recognizable genus and should be accepted as such, type species *Selenomonas palpitans* Simons *ex* Boskamp, 1922, the only species placed in the genus when it was validly published. This species was first described from the contents of the caecum of guinea pigs. A second species that belongs in the genus is *Selenomonas sputigena* (Flügge, 1886) Dobell, 1932. This species occurs in the human mouth and may even have been seen by van Leeuwenhoek in his studies of mouth organisms in 1683. Still a third species has been described by protozoologists as *Selenomonas ruminantium* (Certes, 1889) Wenyon, 1926. It is found in the rumen juice of herbivorous mammals. The genus clearly belongs in the family *Spirillaceae* Migula.

Although *Selenomonas* as proposed by von Prowazek (3) in 1913 has priority over *Selenomastix* that Woodcock and Lapage (17) proposed the same year, the fact that von Prowazek did not name a species as belonging in the genus gives *Selenomonas* the status of a *nomen nudum*. Nevertheless, *Selenomonas* von Prowazek has been accepted by some as having priority (18, 19, 20), and general usage has favored its acceptance. Therefore, *Selenomonas* has been used in this discussion, while awaiting a review of the status of the two names by the International Judicial Commission on Bacteriological Nomenclature.

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ADDENDUM

The pictures on Plate I are photomicrographs of *Selenomonas palpitans*. They show flagella arising from the middle of the concave side of the organism and suggest that their insertion lies very close to, perhaps inside, the nucleus. The photographs reinforce the information contained in drawings of *Selenomonas* in the first detailed account of this species by Boskamp (1922).

All figures are from preparations of the contents of the caecum of healthy guinea pigs.

Figures 1–3. From caecum contents suspended in 5% formalin, washed by centrifugation and stained by Loeffler's method. The cells in figures 2 and 3 are preparing to divide.

Figures 4–8. From wet films on coverslips fixed for 7 minutes in Schaudinn's fixative (without acetic acid). Stained with Giemsa solution. Figures 4 and 5 from films that had been treated for 10 minutes with N/1 HCl at 60 C before staining. Figures 6, 7 and 8 from directly stained films that had been differentiated in 20% alcohol (Dobell, 1911). All Giemsa preparations were photographed mounted in water.

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C. F. ROBINOW,
Department of Bacteriology and Immunology,
University of Western Ontario,
London, Ontario, Canada.

PLATE I